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A Perspective on Future Tiger Shark Research

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This "Perspectives" paper identifies aspects of tiger shark (*Galeocerdo cuvier*) biology that are currently unknown or for which additional data are needed to improve interpretive power. Some of these data gaps may be regional. Technical or methodological approaches to acquiring these data are suggested. Some of these technologies already exist, some are in development and some exist in concept only. Reproductive biology and behavior, social interactions and the behavioral ecology of sub-adults are among the areas identified as deserving of future research effort.

Keywords: tiger sharks, behavior, research perspectives, tracking, ecology, population connectivity

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INTRODUCTION

Tiger sharks (*Galeocerdo cuvier*) are large, iconic predators with a circumglobal distribution in warm waters (Compagno, 1984). They play an important role in ecosystem function (Heithaus and Dill, 2002; Ferreira et al., 2017; *inter alia*) and are among the top three shark species identified in attacks on humans (International Shark Attack File[1]). This paper identifies several aspects of tiger shark biology that are currently unknown or poorly understood and which we believe are critical to our understanding of this important predator. These data gaps may vary regionally. We focus on questions that are specific to tiger sharks and which are amenable to manipulative or empirical field experiments (as opposed to correlative analyses) There may be other fruitful areas for investigation that are not covered here. Tools for investigating the biology of vagile marine species are constantly and rapidly improving. These include increasingly sophisticated molecular techniques, portable analysis units (e.g., ultrasonic scanners) and multi-sensor electronic tags for tracking three-dimensional movements and sampling the environment surrounding the focal animal. We suggest technical solutions or methodological approaches for acquiring data to fill gaps in our knowledge of tiger shark biology. Some of these technologies already exist, some are in development and others currently exist in concept only.

REPRODUCTIVE BIOLOGY AND BEHAVIOR

Topic: Pupping, Mating and Gestation Locations

Tiger sharks have low reproductive output (Simpfendorfer, 1992; Whitney and Crow, 2007) making survival of juveniles (and protection of nursery areas) potentially critical to conservation strategies. Although many shark species utilize specific locations (e.g., coastal embayments or estuaries) as

[1] http://www.floridamuseum.ufl.edu/shark-attacks/

nursery areas (as defined by Heupel et al., 2007), tiger sharks apparently lack well-defined nursery areas (Springer, 1967; Whitney and Crow, 2007; Driggers et al., 2008). For example, catch per unit effort (CPUE) surveys show tiger shark pups and juveniles are widely distributed at depths <100 m along the continental shelf of the southeastern United States with highest CPUE near the "Charleston Bump" (Driggers et al., 2008). It is not known whether this broad distribution of pups results from widespread pupping by adult females or dispersal of pups from more specific parturition sites or an extended pupping season (Driggers et al., 2008). The partial migration of adult females from remote Hawaiian atolls to the main Hawaiian Islands during pupping season (Papastamatiou et al., 2013) suggests that there may be preferred tiger shark pupping habitats in Hawaii but this has not been confirmed. Similarly, if specific pupping sites do exist, it is not known if adult female sharks show repeated fidelity to those sites. Sulikowski et al. (2016) speculate there may be specific gestation grounds in the Bahamas but the wide ranging movements of pregnant sharks in other regions (e.g., Papastamatiou et al., 2013) indicate that, if such behavior exists, it may be regionally specific.

The seasonal timing of tiger shark mating is evident from mating scars on females (e.g., Whitney and Crow, 2007), but very little is known about the nature of mating behavior (see Meyer et al., 2018) or whether or not there are specific mating sites. Tiger sharks seem to be generally solitary, so finding a mate may be challenging unless there are specific locations and times when mating occurs. Within the main Hawaiian Islands, the probability of migration between islands for both adult male and female tiger sharks peaks during the winter mating season as does CPUE for adult males in shallow coastal habitats (Papastamatiou et al., 2013; Meyer et al., 2018; A. Tester unpublished data). These observations, in conjunction with a single observation of a failed mating attempt by a camera-equipped male tiger shark in coral reef habitat (Meyer et al., 2018), suggest shallow coastal areas are mating habitats for Hawaii tiger sharks. There are currently no similar data from other parts of the world.

Future Research

One strategy for addressing the nursery location/depth and gestation grounds questions would be to capture adult female tiger sharks during pupping season, scan them with portable ultrasound equipment to see if they are pregnant (Sulikowski et al., 2016) and, if so, equip these sharks with cameras and accelerometry tags to detect pupping events. These sharks could also be equipped with satellite tags to provide insight into where pupping is occurring. These experiments should be geographically widespread.

A longer-term approach would be development of implantable devices that can detect key aspects of blood chemistry that indicate parturition. These physiological data would be transmitted to an externally mounted pop-off tag which would transmit these data via satellite. This dual internal/external tag technology has been successfully used to detect feeding behavior in several marine species including seals (e.g., Skinner et al., 2014). Similarly, equipping mature males with camera and depth and light level sensor packages during mating season (e.g., Meyer et al., 2018) would be the most direct path to elucidating the location and nature of mating behavior.

Topic: Reproductive Cycle

The reproductive cycle of tiger sharks remains one of the least understood aspects of its reproductive biology. Initial work in this area suggested a biennial reproductive cycle (Rivera-López, 1970; Alves, 1977), and that mating appeared to occur before full-term females had pupped (Branstetter et al., 1987). More recently, Castro (2009) surmised that North Atlantic tiger sharks probably have a gestation period of 12 months, based on the observation of tiger sharks carrying both unfertilized eggs and near-term young in May (boreal spring), indicating that females are possibly reproductively synchronous in this region. Conversely, Whitney and Crow (2007) inferred a triennial breeding cycle for Hawaiian tiger sharks, reporting that the proportion of captured sharks that were pregnant was lower than would be expected for a biennial reproductive cycle. The identification of potential differences in reproductive strategies between Atlantic and Indo-Pacific tiger sharks is critical to inform regional stock assessment and fishery management regimes.

Future Research

Geographically diverse data on the reproductive state of large numbers of mature females is required. To avoid lethal sampling, portable ultrasound equipment could be used to assess pregnancy and in-utero pup sizes. Blood chemistry could be sampled from live sharks to determine temporal changes in hormone levels to deduce reproductive cycle status (Sulikowski et al., 2016).

Topic: Sex Separation and Habitat Partitioning

Sexual segregation occurs among adults of many shark species (Meyer et al., 2009; Papastamatiou et al., 2010) and existing evidence suggests this phenomenon may also occur in tiger sharks (Meyer et al., 2014). Tiger shark sex ratio is reported to be close to 1:1 at birth in Hawaii (Whitney and Crow, 2007), while significantly biased toward females off eastern Australia (1.26:1, Holmes, 2015). Concomitantly catches of adults tend to be heavily female-skewed in most coastal locations (Simpfendorfer, 1992; Wintner and Dudley, 2000; Beerkircher et al., 2002; Meyer et al., 2014; *inter alia*). This is thought to result from adult females occupying coastal areas (where most fishing effort occurs), while adult males occupy more offshore habitats for most of the year (Papastamatiou et al., 2013). It is not known at what age this segregation occurs. Size-specific analyses of catch records off eastern Australia revealed catches of males on near-shore shark control gear declined when males reached >280 cm TL (Holmes et al., 2012), potentially indicating greater offshore habitat selection with the onset of male sexual maturity (L_{50} males = 297 cm TL, Holmes, 2015).

Future Research

To distinguish gender-related habitat segregation from a population-wide disparity in sex ratio, simultaneous fishing should be conducted in inshore vs. offshore habitats at multiple locations around the world. Further size-specific analysis and movement data (e.g., Lea et al., 2018) might reveal the ontogeny of sexual segregation in other regions. Specifically targeting males for future tracking experiments would also elucidate differences in habitat selection.

Topic: Occurrence and Frequency of Multiple Paternity

Many carcharhinid species display multiple paternity which is a strategy to amplify the functional size and diversity of the reproductive population (Daly-Engel et al., 2006). A single study of tiger sharks (using a small sample size) did not detect multiple maternity (Holmes et al., 2018). Given its importance to conservation biology, multiple paternity should be more thoroughly investigated worldwide.

Future Research

Opportunistic tissue sampling of tiger shark pups from known mothers should be conducted on a world-wide scale. Coupled with portable ultrasound equipment, it may be possible to use a biopsy needle to non-lethally sample pups from pregnant females.

POPULATION DYNAMICS AND CONNECTIVITY

Topic: Population Connectivity

Whereas tiger shark populations seem to be distinct among the different oceans, there is still debate about within-ocean population structure and there appears to be a discrepancy between the within-basin population structure indicated by molecular genetics and the large-scale movements of tagged individuals in both the Atlantic and Indo-Pacific Oceans (Holmes et al., 2014; Werry et al., 2014; Lea et al., 2015). A recent analysis using nuclear markers (microsatellites) indicated broad genetic differentiation between the Atlantic and the Indo-Pacific Ocean basins with considerable regional structure within the Atlantic and some structure within the Pacific – including a separate Hawaiian population (Bernard et al., 2016). However, this distinction was not observed in a study using a larger sample size (Holmes et al., 2017). Apparently, roaming individuals provide enough gene flow to maintain large, basin-wide populations. These different results indicate that further connectivity research is warranted globally.

Future Research

Development of single nucleotide polymorphisms (SNP) for tiger sharks would complement microsatellite techniques and increase the power to detect genetic variation and metapopulations, even if sample sizes are small. Continued advances in tagging technology that allow for multi-year tracks of mature sharks (e.g., Lea et al., 2015), coupled with the advancement of molecular analyses, is likely to greatly improve our understanding of sex-biased dispersal, reproductive mixing and other spatiotemporal movement drivers that influence population structure and connectivity. Climate change should see a range extension through pole-ward movements in this species, which may increase the potential for greater *trans*-oceanic movements.

BEHAVIORAL ECOLOGY

Topic: Behavioral Ecology of Pups

Virtually nothing is known about the behavior and habitat use of tiger shark pups during their first years of life including how quickly they disperse from their natal sites, what depths or types of habitat they select or how this changes with ontogeny. We do not know how early feeding experience impacts the feeding strategies of sharks later in their lives.

Future Research

Active acoustic tracking (e.g., Holland et al., 1993) and passive acoustic monitoring using anchored receiver arrays (e.g., Heupel and Hueter, 2001) would greatly improve understanding of the behavior of neonate and juvenile tiger sharks. Young-of-the-year and juvenile tiger sharks are of sufficient body size to carry temperature-depth recorders and accelerometers to better understand three-dimensional spatial use and activity rates. Diet could be estimated using non-lethal techniques including gastric lavage (Bangley et al., 2013) and stable isotope analyses (Kinney et al., 2011). Respirometry experiments and feeding studies with captive juveniles would elucidate daily ration and energetics requirements (Lowe, 2002).

Topic: Offshore Movements of Adults

Satellite telemetry (Lea et al., 2015; Meyer et al., 2018) and catch records (Polovina and Lau, 1993; Domingo et al., 2016) show tiger sharks make offshore migrations in both the Pacific and Atlantic. Adult tiger sharks in the Atlantic undertake repeated annual migrations which track latitudinal shifts in sea surface temperatures (SST) (Lea et al., 2015, 2018). Hammerschlag et al. (2012) correlated oceanic tiger shark movements in the mid-Atlantic with catch rates of pelagic fishes, although the causation is unknown. Intriguingly, some sharks in Hawaii (where there are no large seasonal temperature changes) also make extensive and repeated offshore looping excursions lasting several weeks and covering several hundred kilometers (Meyer et al., 2018). Questions arise as to what are the drivers of these excursions or migrations and what (if anything) the animals are eating mid-ocean? Trophic position varies with location and oceanographic environment and as sharks move between habitats – including nearshore and pelagic realms (Carlisle et al., 2012, 2015; Ferreira et al., 2017) but what they are actually eating in mid-ocean remains largely unknown. It is possible that rafting seabirds are an important component. Other partial migrations may exist within tiger shark populations and may be related to ontogeny or nutritional status although there are no empirical data to support this hypothesis (Gallagher et al., 2017).

Future Research

In concept, sharks equipped with satellite-linked tags to detect feeding events (Meyer and Holland, 2012) would reveal the depth and frequency of offshore feeding events. Animal-borne cameras would further elucidate the behavior. However, the problem comes with catching and identifying which sharks will undertake an offshore excursion after being tagged. Continued, long duration satellite telemetry in different regions will give further insight into temporal stability (or not) of feeding ecology. Identification of isotope or fatty acid signatures specific to seabirds (e.g., Cucherousset et al., 2012) would be a significant advance. The influence of nutritional status on movements is difficult to elucidate because nutritional status may change after a shark is tagged.

Topic: Feeding Ecology and Ecologic Services

Multiple diet studies of adult tiger sharks demonstrate them to be adaptable generalists that exploit a wide variety of prey which can vary both regionally and temporally (Lowe et al., 1996; Simpfendorfer et al., 2001; Dicken et al., 2017; *inter alia*). Recent stable isotope studies (Hussey et al., 2015b; Ferreira et al., 2017) confirm tiger sharks as apex predators but also that they are regionally and temporally adaptable and may function more as mesopredators in certain habitats (i.e., feeding on lower trophic level reef fishes, Ferreira et al., 2017). Additionally, there are observations of tiger sharks acting as facultative scavengers feeding at "bonanza" events such as whale carcasses (Dudley et al., 2000; Clua et al., 2013) and also examples of individuals that apparently target specific prey such as fledgling albatross (Lowe et al., 2006) and nesting sea turtles (Fitzpatrick et al., 2012). Thus, there are several aspects of feeding ecology that remain unknown including questions about the degree of individual feeding specialization (or generalization; Matich et al., 2011) and how these originate (e.g., through experience during ontogeny). Are the various types of feeding strategy related to geographic location and do these lead to the disparate growth rates (Branstetter et al., 1987; Meyer et al., 2014) that have been documented from different regions?

Neither the daily ration nor energetic requirements of adult tiger sharks have been directly measured (Hammerschlag et al., 2013) so their impact on the supporting ecosystem is not well defined. In addition to direct predation, what is the role of tiger sharks in shaping an "ecology of fear" that influences the behavior of other species (e.g., Heithaus and Dill, 2002; Heithaus, 2005; Wirsing et al., 2007; *inter alia*) and how does this relate to individual hunting strategies (Towner et al., 2016)?

Future Research

Meta-analysis of existing diet studies should be conducted to look at regional structure in feeding ecology and there needs to be a broader geographic scope of diet studies, especially from open ocean areas. Extensive use of feeding tags, accelerometers and cameras, especially with longer deployment periods, would capture the daily feeding and energetic intake of these animals and provide insight into the direct and indirect effects they have on disparate habitats. Overcoming the logistical constraints of using swim-tunnel respirometry to measure metabolic rates of large sharks (Payne et al., 2015) would allow empirical measurements of the energy requirements of adult tiger sharks.

Topic: Social Interactions of Adults

Virtually nothing is known regarding the social interactions of adult tiger sharks even though it is known that there can be multiple individuals using the same geographic habitat (Hammerschlag et al., 2017; Meyer et al., 2018). What is the nature and frequency of intra-specific interactions? Is there any evidence of schooling? Do tiger sharks travel together or with other species?

Future Research

Deploying "business card tags" (Holland et al., 2009) on multiple sharks caught in well-defined areas could answer questions regarding the frequency and duration of intra-specific interactions – especially if tags were developed to download archived interaction data to moored receivers. Analyzing these data using network analysis techniques would undoubtedly be productive (Stehfest et al., 2013). Deployment of shark-borne cameras would also be informative.

Topic: Extent of Lateral and Vertical Range and Impacts of Climate Change

Several studies demonstrate linkage between tiger shark distribution and water temperature (Heithaus, 2001; Papastamatiou et al., 2013; Lea et al., 2015, 2018; Payne et al., 2018; *inter alia*). Tiger sharks occupy a broad thermal niche with a preference for temperatures between ∼17°C and ∼28°C (Payne et al., 2018) and migrate in response to changing SSTs. However, the impacts of El Niño Southern Oscillation (ENSO) events are unknown. Overall tiger sharks may be climate change "winners"; they eat a wide variety of prey and are thus protected against climate-change driven demise of any one prey type. Warming SSTs may also extend their range toward the poles (Last et al., 2010; Payne et al., 2018).

Future Research

Electronic tagging studies – both acoustic and satellite-linked – have revealed distributions and aspects of habitat use for multiple species that are not obvious through catch statistics or mark/recapture studies (see Hussey et al., 2015a). The extent of current range and any future changes in distribution may be detectable through the use of long-term acoustic transmitters and the establishment of collaborative acoustic arrays throughout the coastal margins of regions such as North America (Animal Telemetry Network; Block et al., 2016) and Australia (Integrated Marine Observing System Animal Tracking Facility; Hoenner et al., 2018) where they have access to a range of temperatures. The deployment of "oceanography" tags that can document *in situ* temperature, salinity and oxygen levels experienced by the sharks will help to define current physiological tolerance and habitat preferences and inform models of the impacts of climate change. Such data could be used to site future refugia. Satellite tagging of tiger sharks in the eastern Tropical Pacific where ENSO events are most extreme could shed light on their latitudinal range expansion along continental coasts with warming SSTs. A global review of historical and recent catch statistics might detect expansion of range (e.g., Last et al., 2010) and possible abandonment of areas that have become unsuitable (i.e., too hot; Payne et al., 2018).

INTERACTIONS WITH HUMANS

Topic: Ecotourism

Tiger sharks are components of ecotourism activities in multiple locations including Bahamas (Hammerschlag et al., 2012), Fiji (Brunnschweiler et al., 2014), South Africa (Dicken and Hosking, 2009), and Hawaii (Meyer et al., 2009) and shark tourism operations are increasing world-wide. In contrast to significant impacts of shark tourism on white shark (*Carcharadon carcharias*) biology (Huveneers et al., 2018), two studies suggest a limited effect of shark-related ecotourism on tiger sharks (Hammerschlag et al., 2012, 2017). However, these were "indirect" measurements and from a single location. Thus, there is debate as to whether "provisioning" (i.e., chumming) exacerbates the influence (if any) of ecotourism activities on the biology of sharks associated with them.

Future Research

Because the extent of provisioning varies from operation to operation and because they are sited in different environments, impact studies should be conducted on a case-by-case basis. Electronic tagging activities targeting sharks caught at ecotourism sites (e.g., Meyer et al., 2009) would elucidate impacts on their biology. Deploying tags that identify and quantify feeding events (Meyer and Holland, 2012) would be especially useful in assessing the impact of provisioning on the feeding ecology of sharks associated with ecotourism sites.

Topic: Shark Behavior and Public Safety

Worldwide, tiger sharks are the second-most likely to be involved in attacks on humans (13%; International Shark Attack File[2]) and, in some regions such as Hawaii (Division of Aquatic Resources, Hawaii Department of Land and Natural Resources[3]), their impact is considerably greater. Given their generalist diet and the fact that tiger sharks are frequently close to humans it seems surprising that they do not bite humans more frequently. It is possible that there are fine scale (10 or 100 of meters) aspects of tiger shark behavior that reduce their interactions with recreational ocean users. Is there a "no-go" environment (e.g., depth or wave energy) that protects humans most of the time? These fine scale aspects of shark movement should be investigated.

[2] http://www.floridamuseum.ufl.edu/shark-attacks/

[3] http://dlnr.hawaii.gov/sharks/shark-incidents/incidents-list/

Future Research

Active acoustic tracking of adult tiger sharks (Holland et al., 1999) in areas of high human-use would reveal fine-scale aspects of behavior that are not currently known. Double tagging focal animals with long-term transmitters detectable by acoustic receiver arrays would allow merging of fine-scale movement data with long-term habitat use data.

Topic: Sharks as Oceanographers

The use of animal-borne sensors is an emergent field in surveying the physical structure of the world's oceans (e.g., Roquet et al., 2014) and is especially pertinent given the unprecedented rates of change and need for increased monitoring (Abraham et al., 2013). The wide-ranging movements of tiger sharks (both laterally and vertically), their use of both coastal and offshore environments and their ability to tolerate capture and tagging (Gallagher et al., 2014) make them ideal candidates for the role of "sharks as oceanographers". In "proof of concept" experiments, tiger sharks equipped with "oceanography tags" are currently providing near-real time ocean profiles (pers. obs.).

Future Research

Long-term programs that release tiger sharks equipped with "oceanography tags" in various regions could make a significant contribution to our understanding of the physical structure of the world's tropical and semi-tropical oceans, coastal shelves and marginal seas while simultaneously revealing the habitat preferences of this important and iconic species.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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